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Observations on the inception, season, and duration of cambium development in the American larch [Larix laricina (Du Roi) Koch.] *

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(WITH PLATES 18 AND 19)

INTRODUCTORY

During the past twenty-five years very little attention has been devoted to a minute study of the diameter increase in trees. Comparatively little is known concerning the season of wood formation; and with respect to the region of the tree in which diameter increase first begins, the evidence is contradictory. With the object of determining the part of the tree in which cambial activity begins, as well as to determine the season of growth, investigations were begun during the season of 1909 and continued in 1911. The results obtained from the study of material collected these two seasons form the basis of this paper.

The subject was suggested by Prof. W. W. Rowlee, and to him, as well as to Prof. B. M. Duggar, the writer is indebted for helpful suggestions.

HISTORICAL

The work of von Nordlinger, Th. Hartig, Robt. Hartig, Mer, and others has thrown some light upon the extent and duration of cambial activity. They have found, in general, that under forest conditions growth first begins in the youngest twigs and then proceeds downward into the older regions. Less work has been done on the cambial activity in isolated trees.

Concerning the region of first cambial activity, Th. Hartig† concluded that it occurred in the youngest twigs and then gradually extended downward. In a 30-year old *Pinus sylvestris*, and also in oak, cambial activity began almost simultaneously over the entire trunk, while in larch and maple of the same age cambial activity began from two to four weeks later in the lower part of the trunk than in the twigs.

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* Laboratory of Plant Physiology, Cornell University, Contribution No. 8.

† Hartig, T. Anatomie und Physiologie der Holzpflanzen, 368. 1878.

As a result of extensive investigations, Robt. Hartig* advanced the idea that cambial awakening was dependent upon temperature and that therefore the thickness of the bark, temperature of the soil moisture, and insolation, were important factors. He found in an isolated 10-year old *Pinus sylvestris*, that cambial activity had begun two weeks earlier than in isolated 35- and 65-year old trees, and four weeks earlier than in a 100-year old tree grown under forest conditions. The comparisons were all made at a height of 6 meters. He also found that under natural forest conditions the growth of the annular ring of Scotch pine, Norway spruce, and European larch at a height of 27.5 meters, was on June 9 respectively 66 per cent, 56 per cent and 75 per cent completed. Going toward the base the growth decreased, and at a height of 1.5 meters the percentage of the annular ring completed was 35, 21 and 18 per cent respectively. In isolated trees of Scotch pine and Norway spruce the growth on July 9 was approximately the same in all parts of the trunk. Under forest conditions growth was found to begin in the twigs and proceed downward, the cessation of growth following the same order.

According to Mer,† the cambial activity in oak, beech, basswood, fir, and other trees of twenty-five years of age and under begins in the youngest twigs. In older trees cambial activity is described as simultaneous at the bases of the branches and trunk. He states also that in a single cross-section cambial activity may be evident on one side and not on another.

Hastings‡ found that in broad-leaved trees increase in diameter did not begin until the buds had opened. He found that growth first begins in the 1-year old twigs, and later it occurs in 2- and 3-year old twigs. When wood is forming in 5- or 6-year old growth there is simultaneous development over the entire tree. In pine it begins first in the 2- and 3-year old twigs. In the hemlock the growth was first observed in the 6-year old twigs, while in *Taxodium distichum* the same conditions prevail as in the broad leaves.

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* Hartig, R. Das Holz der deutschen Nadelwaldbäume, 35–38. 1885.

† Mer, E. Sur les causes de variation de la densité des bois. Bull. Soc. Bot. France **39**: 95–105. 1892.

‡ Hastings, G. When increase in thickness begins in our trees. Science II. **12**: 585. 1900.

Buckhout* made during a period of four years caliper measurements of European larch at intervals of five days during the growing season. The measurements were made at breast height and the age of trees experimented upon is given as 45 years. He found that the formation of leaves was coincident with the beginning of diameter increase. The beginning of this increase was close to April 25, during the four years. He found a gradual increase from this date until about July 1, when further growth in diameter practically ceased. The data secured from this method of measurement are not, as he himself realized, entirely conclusive, on account of the errors which may result from the swelling and shrinking of wood and bark with the varying moisture content.

From the horticultural side gross investigations have been made by Keffer,† Goff,‡ Cranefield,§ and others on the duration of growth in fruit trees. Their work is concerned with the development of shoots and on the duration of wood increase as determined by the readiness with which the bark could be peeled. The work of these men will be considered in a subsequent paper.

METHODS OF INVESTIGATION

For the investigation during 1909, four larch trees of approximately thirteen years of age were used. These trees are hereafter designated for convenience as trees *A*, *B*, *C*, and *D*. The trees originally grew in a swamp in Oswego County, New York, but were transplanted in 1902 to the nursery on the Cornell University Campus, on land which slopes gently to the west and is of a well-drained, heavy clay soil type. The trees were planted four feet apart and were shaded on the east and west sides but not on the north or south. Trees *B*, *C*, and *D* were very uniform as regards size and form. Tree *A*, although of the same age, was slightly smaller.

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* Buckhout, W. A. The formation of the annual ring of wood in European larch and the pine. Forestry Quarterly **5**: 259–267. 1907.

† Keffer, C. A. The early growth and training of apple trees. Tenn. Agr. Exp. Sta. Bull. **14**: 1–16. 1901.

‡ Goff, E. S. The resumption of root growth in spring. Wisconsin Agr. Exp. Sta. Ann. Rep. **15**: 220–228. 1898.

§ Cranefield, F. Duration of growth period in trees. Wisconsin Agr. Exp. Sta. Ann. Rep. **17**: 300–308. 1900.

In order to determine the region of growth inception it was necessary to take material from the apex of the tree to the base. The larch has, at intervals, whorls of branches, the number of which agree approximately with the age of the tree. The trees used had each ten such whorls and material was removed from below each whorl, at different times throughout the growing season. Cuttings were made only from the south side of each tree. The first cuttings were made a few inches below each whorl of branches and the subsequent cuttings were made a few inches below the preceding and a little to one side. In obtaining the material for study two incisions, 2 cm. apart, were made through the bark and into the wood to a depth of 1 cm. and the piece then removed with a small knife. The injured area was then filled with grafting wax.

The material collected from trees *A* and *B* was fixed in a solution consisting of 33 parts glycerine, 35 parts alcohol, 30 parts distilled water, and 2 parts glacial acetic acid. The material kept in this solution was in excellent condition for sectioning, though, of course, no good fixing of the protoplasmic structure was obtained. That collected from trees *C* and *D* was fixed in Gilson's solution and kept, by mistake, in 95 per cent alcohol. When attempts were made to section it, several months later, considerable difficulty was experienced, because of brittleness. Attempts to soften the material, by allowing it to remain in equal parts of glycerine and alcohol, and also in glycerine alone, proved futile. The greater part of the material was sectioned without imbedding, but some of it was necessarily imbedded in celloidin. The sections were cut from 20 to 40 μ in thickness and stained with safranin and Delafield's haematoxylin of the formula so commonly used for wood staining. The methods employed during the season of 1911 are described subsequently.

INVESTIGATIONS OF 1909

The first cuttings were made on April 19 and at this time the buds located on the 4-, 5-, and 6-year old wood had opened, the leaves being 1/16 of an inch in length. On the younger wood, the buds were less advanced. This was more marked in the 1- and 2-year old wood. This slower development toward the terminal shoot and apex of the branch held true also for the catkins. The same condition was noted also in several larches which in September produced a new growth of leaves, the result of a drouth, followed by favorable conditions. This earlier development of leaves on the older wood is significant in the light of the subsequent facts concerning the inception of cambial activity.

Cambium in resting condition.—According to Sanio and other investigators the cambium proper consists of a tissue but one cell in thickness, which cells by division produce a row of xylem mother and a row of phloem mother cells. Each of these rows divides and gives rise respectively to two rows of potential xylem cells and two rows of potential phloem cells. Except by careful cytological study the row of true cambium cells cannot be distinguished from the neighboring cells. The term cambium has been, therefore, generally applied to that tissue which lies between the visibly differentiating phloem and xylem. The cambium tissue is composed of a number of rows of cells, which cells are characterized by their thin walls, dense protoplasmic content, and, viewed in cross section, rectangular shape. In trees in the resting condition it would be reasonably assumed that the true cambium comprises the first row of cells just without the xylem. The cells bordering this row on the outside would then be considered as phloem. As a matter of fact, however, sections made from cuttings obtained from the trunk of larch on November 13 exhibit just outside of the xylem a distinct tissue 34 μ in diameter, consisting of five or six rows of cells in thickness. The cells of the outer five rows are not visibly distinguished from cells of the inner row, but are distinguished from the adjacent phloem cells by their size and protoplasmic content. See FIG. 1 and 3. Because of the similarity of all of these cells I have considered the six rows as comprising the cambium tissue, the term cambium being employed in its generally applied sense.

Inception of cambial activity and development of phloem.—The material collected on April 19 showed that cambial activity had begun. The layer of six cambium cells had increased in diameter.

The outer cells of this tissue were losing their rectangular shape and assuming more nearly that of a square, as viewed in a cross section. See FIG. 1, 2, and 3. In studying the slides made from material collected on April 19, it was found that in the 5th, 6th, and 7th cuttings of tree *A* the cambium had developed to a greater extent than in the other cuttings. Not only had the cambium increased in diameter, but seemingly new cells had been formed. This increased development near the middle was maintained until May 25. The average increase in number of phloem cells by May 25 was only 1.8, but the diameter increase of the cambium and phloem was nearly 100 per cent. Up to this time no xylem whatsoever had been developed. It appears therefore that the earliest growth consists in an enlargement of the cambium tissue with the gradual transformation of the peripheral cells into phloem tissue. The old phloem cells adjacent at this time are becoming compressed due to the pressure brought about by the transformation of the cambial cells. Compare FIG. 1, 2, and 3.

In TABLE I are given the figures obtained by the measurement of the diameter of phloem and cambium tissues in trees *A* and *C*. The figures for the diameter of the cambium tissue during the resting period (cutting made November 13) are given for comparison. The figures included under the dates April 19 to May 25 inclusive refer to tree *A*. From June 3 to July 6 the figures refer to tree *C*.

As indicated previously, the six-celled layer adjacent to the xylem is considered the cambium. Although transformation of the peripheral cells had occurred, it is difficult to state which cells are cambium and which cells are phloem. Consequently the six rows, despite the transformation, I have considered as cambium. Any cells in excess of the six rows, which lie within the old compressed phloem cells, I have considered as new phloem. After May 25, when xylem and phloem were both developing rapidly, the cambium tissue was still considered as a tissue of six rows of cells. It was difficult to select always the six most uniform rows, but in general the error was slight and at most of little consequence.

From an examination of the table it may be seen that up to May 25 the middle regions show the greatest growth. From April 19 to May 25 the increase in phloem was gradual, but from May 25

TABLE I

NUMBER OF ROWS OF NEW PHLOEM CELLS AND DIAMETER OF PHLOEM AND CAMBIUM TISSUE IN TREES *A* AND *C*

Region of cutting	Nov. 13		Apr. 19		Apr. 26		May 5		May 11		May 25		June 3		June 15		June 30		July 6	
	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ
Below 1st whorl	0	34	0	34	0	34	0	41	0	58	0	51	7	122	7	146				
Below 2d whorl	0	34	0	54	0	58	1	51	0	58	0	51			9	170				
Below 3d whorl	0	34	0	58	1	68	0	58	0	51	4	75			10	184	12	224		
Below 4th whorl....	0	34	2	58	1	61	0	51	2	68	4	75	10	187	8	184	15	296		
Below 5th whorl....	0	34	1	68	2	71	2	71	3	74	3	85	11	204	9	177	14	278		
Below 6th whorl....	0	34	2	61	1	68	2	74	2	71	3	75	12	221	9	211	14	273		
Below 7th whorl....	0	34	1	68	1	65	1	58	1	68	2	61	11	207	9	191	13	262		
Below 8th whorl....	0	34	0	58	0	48	1	51	1	61	2	58	14	190	14	211	14	278	15	278
Below 9th whorl....	0	34	0	44	0	51	0	51	1	54	0	51	—		11	208		—	16	289
Below 10th whorl...	0	34	0	44	0	51	0	44	0	51	0	51	12	204	10	204		—	12	238
Average.........	0	34	0.6	54.7	0.6	57.5	0.7	55	1.	61.4	1.8	63.3	11	190.7	9.6	189	13.6	268	14.3	268

to June 3 the growth was markedly increased, while from June 3 to June 15 seemingly little growth occurred. After June 3 it appears that relatively few new phloem cells were formed, but growth consisted more of an enlargement of the cells already formed. Some of the figures for June 15 are less than the corresponding figures for June 3. This may be perhaps explained by the fact that the cuttings were made somewhat lower, or better perhaps by the fact that in obtaining these cuttings they were not taken on a line directly below the preceding, but to one side. Mer (loc. cit.) draws special attention to the well-known observation that wood growth is not always uniform on all sides of the tree.

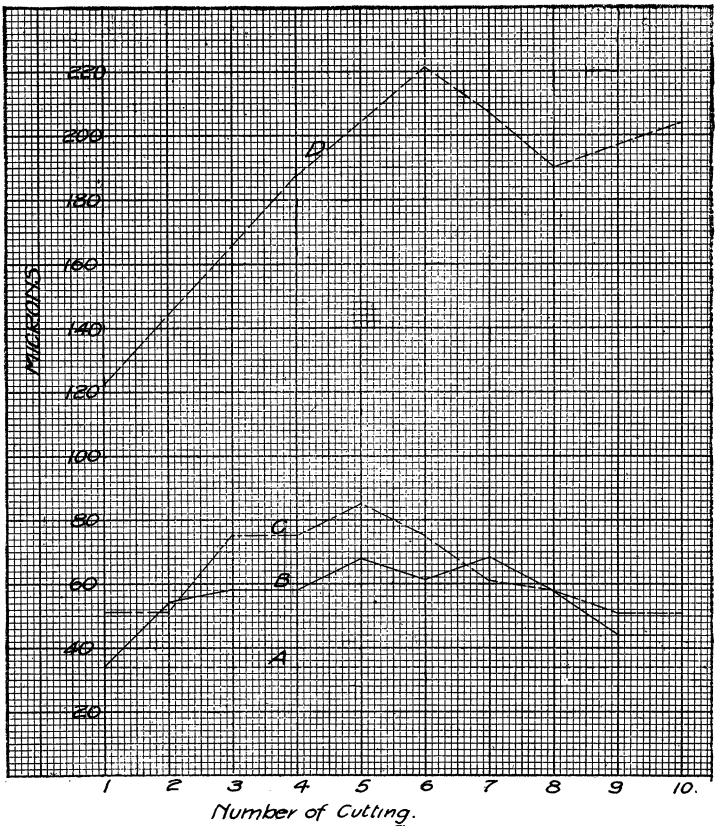

DIAGRAM I. Diameter of cambium and new phloem at various different dates. *A*, Nov. 13; *B*, April 19; *C*, May 25; *D*, June 3.

By July 6 the phloem was nearly complete with respect to cell numbers; for, the average annual number of rows of phloem cells produced during a period of three years was found to be seventeen. At this time the cells were all very regular in form and no visible differentiation had occurred. In DIAGRAM 1 are represented the diameter measurements of the phloem at several different dates.

In trees *B* and *D* the growth is similar to that in trees *A* and *C*, though more vigorous growth resulted in tree *B* than in tree *A*. In this tree also the development of cambium consists first in a transformation of the peripheral cells. In this case, however, the number of rows of phloem cells produced by May 25 was 5.6 with nearly a 200 per cent increase in diameter. The detailed figures are given in TABLE II.

TABLE II

NUMBER OF ROWS OF NEW PHLOEM CELLS AND DIAMETER OF PHLOEM AND CAMBIUM TISSUES IN TREES *B* AND *D*

Region of cutting	Nov. 13		May 5		May 11		May 25		June 8		June 18	
	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ
Below 1st whorl.....	0	34	—		—	75	2	68	8	170	11	228
Below 2d whorl	0	34	0	34	3	58	4	122	11	193	11	218
Below 3d whorl	0	34	3	68	4	82	4	76	—	—	11	286
Below 4th whorl.....	0	34	4	102	4	102	6	92	12	221	14	262
Below 5th whorl.....	0	34	5	85	6	115	—	—	—	—	12	262
Below 6th whorl.....	0	34	4	68	8	107	7	92	10	190	13	238
Below 7th whorl.....	0	34	—	—	4	85	7	102	—	—	14	279
Below 8th whorl.....	0	34	4	85	—	—	6	92	8	170	—	—
Below 9th whorl.....	0	34	2	61	—	—	6	76	8	173	12	245
Below 10th whorl....	0	34	3	75	—	—	6	—	—	—	11	238
Average........	0	34	3.1	72	4.8	89	5.3	90	9.5	186	12	250

Development of xylem.—While in tree *A* there was a gradual increase in phloem from April 19 to May 25, yet no xylem cells had been formed. During the week of May 25 to June 3, coincident with the marked increase of phloem, a very marked increase of xylem occurred, over one third of the xylem being completed during these seven days. TABLE III gives the figures obtained for the number of rows of xylem cells formed, and the diameter of the xylem tissue in the various cuttings at the different dates. There is included also the diameter of the xylem tissue formed in tree *B* during the years 1909 and 1910. In the first column the figures refer to tree *A*. The figures from June 3 to July 6 refer to tree *C*.

TABLE III

NUMBER OF ROWS OF NEW XYLEM CELLS FORMED AND DIAMETER OF NEW XYLEM TISSUE IN TREES *A* AND *C*

Region of cutting	May 25	June 3		June 15		June 30		July 6		1909	1910
	No.	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	Dia. μ	Dia. μ
Below 1st whorl ..	0	15	262	25	544	43	1,054			646	986
Below 2d whorl ..	0			33	833	55	1,564			1,598	1,377
Below 3d whorl ..	0	20	578	33	918	48	1,462			1,853	1,870
Below 4th whorl..	0	29	697	43	1,122	50	1,462			1,785	1,870
Below 5th whorl..	0	28	748	45	1,292	55	1,530			1,360	1,955
Below 6th whorl..	0	23	646	46	1,326	58	1,666			1,275	1,224
Below 7th whorl..	0	24	648	36	1,122	57	1,515			1,734	1,428
Below 8th whorl..	0	22	714	36	1,156	57	1,632	65	1,972	2,363	1,598
Below 9th whorl..	0	—	697	28	850		—	62	1,870	1,666	1,088
Below 10th whorl.	0	20	663	27	833	58	1,564	58	1,802	—	—
Average.......	0	22.5	628	35.2	999.6	53.3	1,493	61.6	1,881	1,586	1,488

From the table it cannot be determined exactly in which part of the tree xylem growth first begins. The greatest growth by June 3 was below the fifth whorl of branches while the least growth was just below the first whorl of branches. In general, by June 3 more xylem cells were formed in the middle of the tree than at either the top or base. This would tend to indicate that the first growth of xylem occurred in the middle of the tree below the fifth whorl of branches.

TABLE IV

NUMBER OF ROWS OF NEW XYLEM CELLS AND DIAMETER OF NEW XYLEM TISSUE IN TREES *B* AND *D*

Region of cutting	May 11	May 25		June 8		June 18	
	No.	No	Dia. μ	No.	Dia. μ	No.	Dia. μ
Below 1st whorl.............	0	0	0	22	442	43	1,003
Below 2d whorl..............	0	0	0	40	647	53	1,326
Below 3d whorl..............	0	0	0	—	—	55	1,394
Below 4th whorl.............	0	4	51	35	918	50	1,258
Below 5th whorl.............	0	—	—	—	—	45	1,292
Below 6th whorl.............	0	5	55	32	850	46	1,122
Below 7th whorl.............	0	2	20	—	—	55	1,258
Below 8th whorl.............	0	0	0	34	850	—	—
Below 9th whorl.............	0	0	0	30	782	50	1,292
Below 10th whorl............	0	0	0	—	—	49	1,292
Average..................	0	1.2	14	32	748	49	1,248

TABLE V

TOTAL NUMBER OF ROWS AND DIAMETER INCREASE OF PHLOEM, CAMBIUM, AND XYLEM CELLS IN TREES *A* AND *C*

Region of cutting	Nov. 13		Apr. 19		Apr. 26		May 5		May 11		May 25		June 3		June 15		June 30		July 6	
	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ
Below 1st whorl....	6	34	5	34	5	34	7	41	7	58	6	51	28	384	38	690	—	—		
Below 2d whorl	6	34	6	51	7	54	6	51	6	58	6	51	—	—	48	1,003	—	—		
Below 3d whorl	6	34	6	51	6	58	6	58	6	51	10	75	—	—	49	1,101	66	1,686		
Below 4th whorl....	6	34	8	68	6	62	8	51	8	68	10	75	45	884	58	1,305	71	1,758		
Below 5th whorl....	6	34	7	61	8	71	9	71	9	68	9	85	45	952	60	1,468	75	1,741		
Below 6th whorl....	6	34	7	75	8	68	8	75	8	71	9	75	41	867	62	1,536	78	1,945		
Below 7th whorl....	6	34	7	58	7	65	7	58	7	68	7	61	41	853	53	1,312	76	1,842		
Below 8th whorl....	6	34	6	51	7	48	7	51	7	61	7	58	42	935	56	1,332	77	1,910	86	2,251
Below 9th whorl....	6	34	6	44	6	51	7	51	7	54	6	51	—	—	45	1,057	—	—	84	2,125
Below 10th whorl...	6	34	6	44	6	51	6	51	6	51	6	51	38	867	43	1,037	—	—	76	2,040
Average.........	6	34	6.4	53.7	6.6	56	7.1	55.8	7.1	60.8	7.5	63.3	40	820	51.2	1,184	73.8	1,813	82	2,138

While in trees *A* and *C* the region of the first growth of xylem could not be definitely located, more fortunate results were obtained with tree *B*. No xylem was formed in tree *B* until May 25 and then neither at the top nor at the base of the trunk, but in the middle region. By May 25 then the xylem in that part of the tree between the fourth and fifth whorls of branches was four cells in thickness,—while between the sixth and seventh whorls it was five cells and between the seventh and eighth it was two cells in diameter. The most marked development again occurred immediately after May 25. The detailed figures are given in TABLE IV.

Season and duration of diameter increase.—In order to bring out more clearly the period of greatest diameter increase, the combined values for increase of phloem, cambium, and xylem, in trees *A* and *C* are given in TABLE V.

From the table it is at once evident that very little growth took place previous to May 25, and the growth which occurred was confined, as before indicated, entirely to the cambium and phloem. From May 25 to June 3 a very marked increase occurred, and during that time in the middle regions of the trunk nearly one half of the total diameter increase was completed. In TABLE VI is given the daily average increase in rows of cells and also the daily diameter increase in trees *A* and *C*.

TABLE VI

Period	May 25–June 3	June 3–June 15	June 15–June 30	June 30–July 6*
No. rows of cells	4.2	1.	1.4	1.
Dia. in microns	94.5	30.	40.	48.

By July 6 the ring of xylem was almost complete, judging from the extent of the summer wood which was then in the process of formation, though not yet completely developed. Unfortunately no further series of cuttings were made after July 6 to determine the succession with regard to growth cessation.

In TABLE VII is given the combined diameters of the phloem, cambium, and xylem tissue in trees *B* and *D*, as well as the total number of cells.

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* For cutting nos. 9–10 only.

TABLE VII

TOTAL NUMBER OF NEW ROWS AND DIAMETER OF PHLOEM, CAMBIUM AND XYLEM CELLS IN TREES *B* AND *D*

Region of cutting	Nov. 13		May 5		May 11		May 25		June 8		June 18	
	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ
Below 1st whorl....	6	34	—	—	10	75	8	68	36	612	60	1,231
Below 2d whorl....	6	34	6	34	9	58	11	89	57	840	70	1,544
Below 3d whorl....	6	34	9	68	10	88	10	75	—	—	72	1,680
Below 4th whorl...	6	34	10	102	10	102	16	143	53	1,071	70	1,520
Below 5th whorl....	6	34	11	85	14	115	—	—	—	—	63	1,486
Below 6th whorl....	6	34	10	68	15	108	18	147	48	1,040	65	1,506
Below 7th whorl....	6	34	—	—	11	85	14	122	—	—	77	1,537
Below 8th whorl....	6	34	10	85	—	—	12	92	48	986	—	—
Below 9th whorl....	6	34	8	61	—	—	12	76	44	955	68	1,537
Below 10th whorl...	6	34	9	75	—	—	—	—	—	—	62	1,530
Average........	6	34	9	72	11	90	12.6	101.5	47.5	917	69.4	1,508

The season of diameter growth in larch is relatively short. Practically all of the growth occurred during the month of June. The small increase produced from the time of bud opening, April 19 to May 25, consisted entirely of cambium and phloem development. The diameter increases of trees *A* and *C* and *B* and *D* during the season 1909 are graphically represented in DIAGRAM II.

INVESTIGATION OF 1911

Since the studies made in 1909 indicated that growth in diameter first occurred in the middle region of the trunk and not at the base or apex, it seemed advisable to continue these studies with respect to the development in the lateral branches. The investigation was made with the object of answering the three following questions: (1) Does inception of diameter increase begin first in the topmost branches, in the middle, or in the basal, branches? (2) In what part of the individual branches does diameter increase begin? (3) Does xylem development in the lateral branches precede that in the trunk?

For this investigation a larch tree of approximately 10 years of age was used. It was growing isolated, about 100 feet from the trees mentioned above, growing in the nursery row. For convenience this tree is hereafter designated as tree *E*. On May 22, from each of the whorls of branches from apex to base, one branch

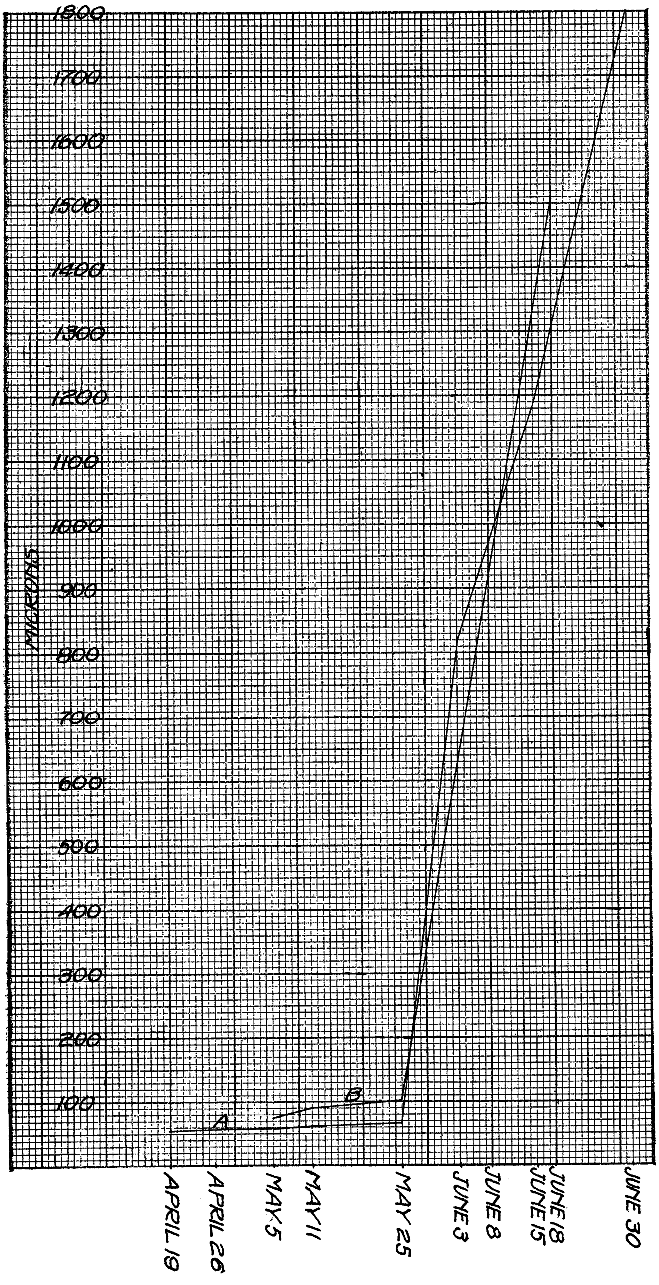

Diagram II. *A*, diameter increase in trees *A* and *C*; *B*, diameter increase in trees *C* and *D*.

was removed. The removal, as before, was made from the south side of the tree. The branches were numbered according to their position on the tree, the topmost branch being No. 1, and the basal branch No. 7. From the individual branches there was removed from each season's growth a cutting; from the topmost branch two such cuttings were removed and from the basal branch seven cuttings. These cuttings were fixed, sectioned, and prepared as before. In the following table the figures given refer only to the number of cells in the new xylem layer and to the diameter of that tissue. The diameter increase over the entire tree is represented in DIAGRAM III.

TABLE VIII

NUMBER OF ROWS OF XYLEM CELLS AND DIAMETER INCREASE OF XYLEM TISSUE IN THE CUTTING FROM LATERAL BRANCHES OF TREE *E*

No. of branch	Region of cutting on lateral branch	No. of rows of new xylem cells	Diameter increase of xylem
1	Below 1st whorl	0	0
1	Below 2d whorl	0	0
2	Below 1st whorl	0	0
2	Below 2d whorl	0	0
2	Below 3d whorl	0	0
3	Below 1st whorl	2	37 μ
3	Below 2d whorl	2	37 μ
3	Below 3d whorl	0	0
3	Below 4th whorl	0	0
4	Below 1st whorl	2	37 μ
4	Below 2d whorl	1	18 μ
4	Below 3d whorl	2	37 μ
4	Below 4th whorl	0	0
5	Below 1st whorl	2	29.6 μ
5	Below 2d whorl	1	18 μ
5	Below 3d whorl	0	0
5	Below 4th whorl	2	37 μ
5	Below 5th whorl	0	0
5	Below 6th whorl	0	0
6	Below 1st whorl	2	37 μ
6	Below 2d whorl	0	0
6	Below 3d whorl	0	0
6	Below 4th whorl	1	18 μ
6	Below 5th whorl	2	37 μ
6	Below 6th whorl	0	0
6	Below 7th whorl	2	18 μ
7	Below 1st whorl	0	0
7	Below 2d whorl	0	0
7	Below 3d whorl	1	18 μ
7	Below 4th whorl	0	0
7	Below 5th whorl	1	18 μ
7	Below 6th whorl	0	0
7	Below 7th whorl	0	0
7	Below 8th whorl	0	0

In order to show more clearly the results obtained and to aid in the interpretation the following two tables have been compiled from the preceding. In the TABLE IX are presented for each of the branches the average number of rows of xylem cells and the average diameter increase of the xylem tissue for the entire lateral branch. The averages are obtained from the figures for each individual cutting.

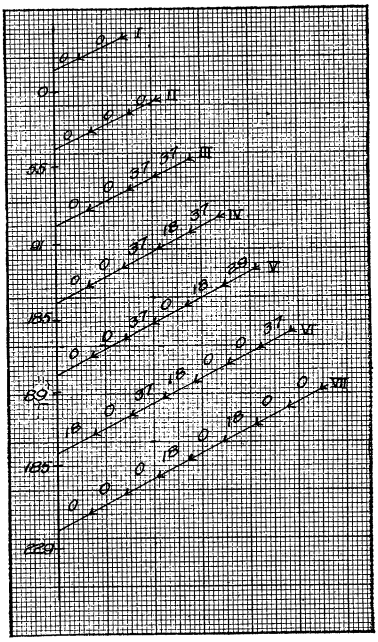

DIAGRAM III. Diameter increase of xylem in various parts of tree *E* on May 2

TABLE IX

AVERAGE DIAMETER INCREASE OF XYLEM IN LATERAL BRANCHES

Branch	Average no. of rows of new xylem cells	Average diameter increase of xylem
I	0	0 μ
II	0	0 μ
III	1	18 μ
IV	1.25	23 μ
V	0.83	14.1 μ
VI	1	15.7 μ
VII	0.25	4.5 μ

From the above table it is evident that the least growth occurred in the top and basal branches and the greatest growth in the middle branches. This increase corresponds with the results secured previously on the diameter increase in the trunk, in which it was found that the growth first began in the middle region.

In regard to the second question as to the region of the branch in which growth first occurs, TABLE X is suggestive. The figures of the following table are the averages of the seven apical cuttings, the seven basal cuttings and the average diameter of xylem in the middle regions of the seven branches.

TABLE X

AVERAGE DIAMETER INCREASE OF XYLEM AT APEX, MIDDLE, AND BASE OF ALL LATERAL BRANCHES

Region of cutting	Diameter increase of xylem
Apical	20.8μ
Middle	7.5μ
Basal	2.5μ

From previous results it was expected that the growth would first occur in the middle of the branch, but the evidence indicates that the development of xylem in the lateral branches begins at the apex and then continues towards the base. The opening of the buds, however, does not follow the same order. On April 26, 1911, the lateral branches of a tree in the nursery row were examined and it was found that buds on the one and two years old wood had not yet opened, on the third year wood the leaves were just protruding while on the older wood the buds were fully opened.

In regard to the third question, " Does diameter increase in the twigs and branches precede that in the trunk?" the following observations were made. From the same tree from which the cuttings from the lateral branches were removed and on the same day,—namely, May 22, cuttings were removed from the apex to the base of the trunk. Seven such cuttings were removed from the south side of the tree, one cutting just below each whorl of branches. From a study of slides prepared from the material the following figures have been obtained. (See TABLE XI.) There are also included in TABLE XI figures derived from cuttings made on June 6.

A comparison of the figures for May 22 with the figures for growth in the lateral branches (see DIAGRAM III) reveals the fact

TABLE XI

NUMBER OF ROWS OF XYLEM CELLS AND DIAMETER INCREASE OF XYLEM IN TREE *E*

Region of cutting	No. May 22	Diameter increase of xylem May 22	No. June 6	Diameter increase of xylem June 6
Below 1st whorl ...	0	0	——	——
Below 2d whorl ...	3	55.5 μ	5	111 μ
Below 3d whorl ...	5	91 μ	7	139.5 μ
Below 4th whorl...	7	185 μ	——	——
Below 5th whorl...	4	88.8 μ	9	259 μ
Below 6th whorl...	7	185 μ	17	444 μ
Below 7th whorl...	9	229.4 μ	20	481 μ
Average..........	5.8	139 μ	9.8	286 μ

that except for the apical part of the trunk the growth there has been much greater than in the branches. The average diameter increase of xylem in all the branches was by May 22 only 10.7 μ, and the average number of cells in the new xylem layer only 0.62. The greatest diameter increase in the branches was only 37 μ, while the average for the trunk was 5.8 cells with a diameter of 139 μ. If reference is made to TABLE VIII it will be seen that no growth occurred in branch No. 2 while in the trunk at this region the increase was 55.5 μ. The average diameter of xylem in branch No. 7 was only 4–5 μ, while in the region of the trunk from which the branch was secured the diameter increase amounted to 229 μ. It is very evident, therefore, that in a larch of this age under isolated conditions growth does not begin first in the twigs and then extend to the trunk, but rather it begins first in the trunk.

The figures in TABLE XI give no strong indication of the region in which growth first began. The diameter increase was greatest just below the 4th, 6th, and 7th whorls of branches. No increase was manifest near the apex.

TABLE XII

Region of cutting in trunk	No. of rows of xylem cells	Dia. increase of xylem
Below 1st whorl.............	Cutting lost	——
Below 5th whorl.............	4	111 μ
Below 7th whorl.............	9	222 μ
Below 9th whorl.............	5	129 μ

In order further to check the work of 1909 a few cuttings were made from another tree in the nursery row on May 22. This tree was now approximately 15 years of age. Cuttings were removed from the south side of the trunk below the 1st, 5th, 7th, and 9th whorls of branches. The results from the measurement of the xylem are found in TABLE XII.

While no conclusions can be drawn respecting the inception of growth the indications again point to the middle region. The figures are of interest mainly because of the fact that growth of xylem has occurred before May 25, which was the date of xylem development in 1909.

FACTORS INFLUENCING DATE OF XYLEM FORMATION

Temperature, moisture, and insolation are important factors in all growth phenomena. In 1909 and 1911 the opening of buds of larch began April 19. In 1909 the xylem formation began on May 25, while in 1911 the xylem formation began about May 20.* The temperature, moisture, and sunshine figures for the intervals between the bud opening and wood formation are found in the following table. The mean temperature for the day is considered as the number of heat units for that day, and the total heat units† is considered as the sum of these mean temperatures.

Period	Total heat units	Hours of sunshine	Precipitation
April 19—May 25, 1909...	1,810	234.5	2.89
April 19—May 20, 1911...	1,769	257.	2.00

The number of heat units then during the interval before wood formation in 1911 was almost as great as that during the longer period of 1909, while the amount of sunshine was greater during the 1911 period. The amount of precipitation at this time of the year was not important as sufficient water was available both seasons. In 1911, however, the mean temperature for the three days preceding wood formation ranged from 76° F.–78° F. and for the three days preceding this period the range of the mean temperatures was 62° F.–69° F. During 1909 the nine days preceding wood formation ranged in mean temperature from 50° F.–54° F. except one day which had a mean temperature of 58. The three days preceding wood formation in 1909 had 39.4 hours of sunshine; the same period in 1911 had 26.2 hours of sunshine. It is very probable therefore that during 1911 the relatively higher temperature for the six days preceding wood formation was important in hastening the inception of xylem formation.

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* The exact date of xylem formation was not determined. The observation on May 22 showed a diameter increase of 6 cells.

† No daily mean temperature was below 34° F.

SUMMARY

RESULTS OF 1909. (1) *Cambium and phloem development.*—The cambium in the trunk during the resting condition consists of six rows of cells 34 μ diameter. On April 19 the first material collected exhibited an increase in diameter of the cambium tissue. The cambium cells were all enlarged while the outer cells were in the process of transformation, changing from a rectangular to square shape as viewed in cross section. In the middle regions of the trunk on April 19 an increase in phloem cells was evident. The increase of cambium and phloem was gradual over the entire trunk in tree *A* up to May 25, the greatest increase being maintained in the middle region. Similar conditions were found in tree *B*, though here the increase of new phloem cells was more marked. The greatest growth of phloem occurred immediately after May 25 and was coincident with the greatest development of xylem.

(2) *Xylem development.*—In tree *A* no xylem was formed before May 25. In tree *B* a few xylem cells were formed by May 25 in the middle regions of the trunk. Growth of xylem was almost simultaneous, however, in all parts of the trunk. The greatest growth occurred immediately after May 25 and in tree *C* the xylem was nearing completion by July 6.

RESULTS OF 1911.—(1) Growth in diameter in the lateral branches begins first in the middle branches and is followed by that in the basal and apical branches.

(2) In the individual branches growth begins first at the apex and then descends towards the base.

(3) Diameter increase of the trunk precedes that in the branches and twigs.

(4) Temperature and insolation conditions in 1911 induced wood formation five days earlier than in 1909.

(5) No direct evidence was secured in 1911 concerning the

region in the trunk of first cambial activity. Indications pointed again to the middle and basal regions.

DISCUSSION OF RESULTS

In a number of anatomical text books it is stated that the xylem development precedes that of the phloem. This idea is conveyed rather ambiguously by Stevens.* In the American larch the development of phloem certainly precedes that of xylem and its most rapid development is coincident with that of the xylem. Brown's† figures indicate that in *Pinus rigida* a similar condition prevails.

The results obtained by the writer do not agree with those of Th. Hartig‡ with 30-year old European larch, wherein diameter increase near the base of the trunk was two to four weeks later than that in the twigs and branches. The factors which may operate to cause this difference are considered subsequently. My results agree with those of Brown§ who finds that in *Pinus rigida* the first diameter increase of xylem begins a few meters below the apex. The work of Brown was done during the same period as that of the writer and on trees in a plot adjacent to those used in this investigation.

Respecting the date of diameter increase Buckhout states that in European larch it is coincident with leaf formation. It is very probable that the diameter increase at this time is due mainly to a swelling of the tissues. In my investigations the development of xylem began a month later than the beginning of leaf formation. From observations made during the past two years with a considerable number of trees and from the results of other investigators it seems probable that in general growth in diameter does not begin until the leaves have been fully developed and have been sufficiently active in food making to supply the requirements of rapid cell formation. The reserve foods stored up in the fall are probably largely utilized in leaf and also in blossom formation, when the latter precede the formation of leaves.

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* Stevens, W. C. Plant anatomy, 2nd Ed., p. 170. 1910.

† Brown, H. P. Growth studies in forest trees, I. *Pinus rigida* Mill. Bot. Gaz. 54: 386–402. 1912.

‡ Hartig, T., loc. cit.

§ Brown, H. P., loc. cit.

What factors operate to cause growth inception in a particular part of a tree? Robt. Hartig* believed that temperature was the most important factor, consequently insolation, temperature of the air and of the soil moisture, and thickness of the bark are the essential factors which determine the region of first diameter increase. No doubt these factors are important, as considerable evidence indicates that in old trees diameter increase is delayed at the base of trunk where insolation is poor and the bark is thick. In young trees, however, these are not the only factors. In the larch trees of 13 years of age the diameter increase did not begin first in those regions with the thinnest bark and best insolation. The thickness of the bark at the apex, middle and base of the tree *A* was respectively 596 μ, 1,937 μ, and 3,278 μ. So also in the isolated tree *E* the inception of diameter increase did not occur in the parts of the tree best insolated and with the thinnest bark, but rather in the thicker barked and more poorly insolated parts of the tree, namely the middle and basal regions of the trunk. In the individual branches, however, growth in diameter began in the regions of thinnest bark and of best insolation.

Whitten† has shown that the color of the bark may be important in the time of growth inception of buds. The color of the bark may be a factor in determining the region of diameter increase in young trees of larch. The color of the bark of the apical part of the trunk in spring is yellowish to greenish, becoming darker towards the base. The darker color, because of its capacity for heat absorption, may counteract the insulating effect of the thick bark, consequently the diameter increase begins in the basal and middle regions. The growth begins first in the middle regions because the bark here is of the same color as that of the basal regions and is only about half as thick. The fact that in the branches and twigs of larch the opening of buds on the apical regions is retarded is suggestive of the influence of the color of the bark. The bark of the apical regions being of lighter color less heat is absorbed, its temperature therefore is lower and the development of the buds is slower. This is in agreement with the

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* Hartig, R., loc. cit.

† Whitten, J. C. Winter protection of the peach. Missouri Agr. Exp. Sta. Bull. 38: 140–164. 1897.

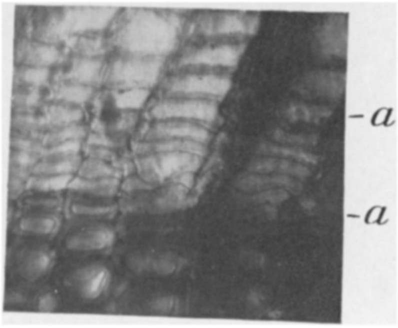

FIG. 1

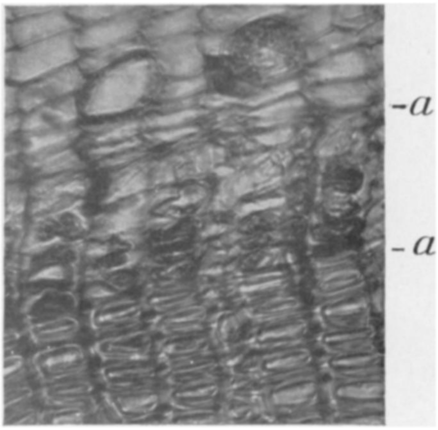

FIG. 2

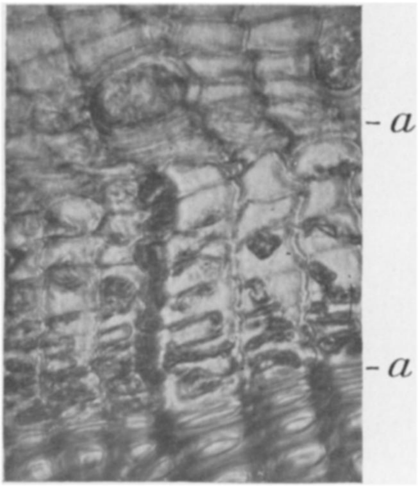

FIG. 3

KNUDSON: CAMBIUM IN THE AMERICAN LARCH

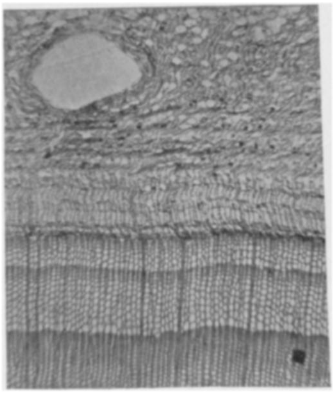

FIG. 4

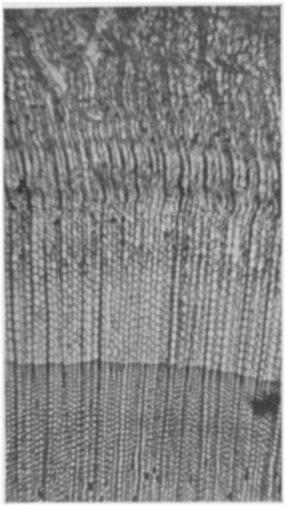

FIG. 5

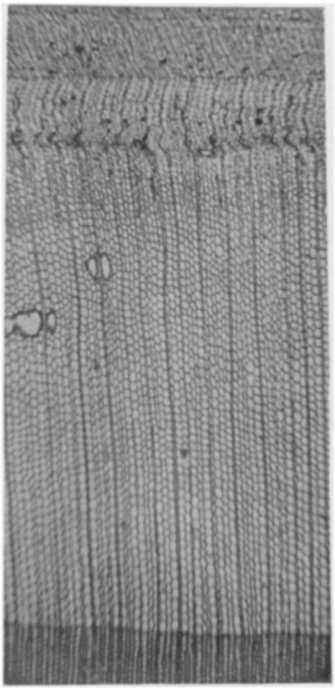

FIG. 7

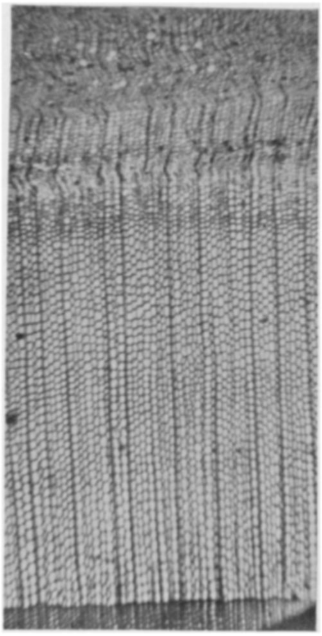

FIG. 6

KNUDSON: CAMBIUM IN THE AMERICAN LARCH

results obtained by Whitten* on the date of blossoming of green- and purple-twigged peach trees.

The temperature of the soil moisture and of the air, and the thickness and color of the bark are not the only factors operative in inducing diameter increase. Certainly as regards all of the above factors the branches are all more favored than the trunk of the tree, yet in the isolated tree *E* the diameter increase began first in the trunk. Food supply may be a factor in stimulating the cambium of the trunk to diameter increase, before there is development in the branches. It is not possible to state the influence of food supply. Controlled experimental work with this as well as with the other factors is necessary to give an idea of the influence of each in stimulating the cambium to activity.

In conclusion it should be stated that considerably more work is necessary in order to establish the region of the tree in which cambium activity first begins. No doubt different conditions will be found for trees of the same species of different ages, and for trees of different species and genera. Investigations of this character are important because only by such studies can the factors be determined which stimulate cambium activity. It is essential also to determine the period and extent of phloem and xylem formation in trees and the duration of cambium activity. Much more work remains to be done along this line. Such work is of especial importance in fruit culture and in a subsequent paper the results of such an investigation will be presented.

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Explanation of figures

FIG. 1. Cutting no. 6 made from trunk on November 13, showing cambium tissue *a* to *a*, consisting of six rows of cells; ×475.

FIG. 2. Shows extent of cambium in basal cutting, No. 10, made on May 5. Compare with Fig. 2; ×475.

FIG. 3. Cutting no. 6 taken from trunk of tree *A* on May 5. Cambium *a* to *a*. Note the increased diameter and cell differentiation; ×475.

FIG. 4. Cutting no. 5 made on May 25 from tree *A*. Xylem formation not yet begun; ×33.

FIG. 5. Cutting no. 4 from tree *C* made on June 3; ×33.

FIG. 6. Cutting no. 7 from tree *C* made on June 30; ×33.

FIG. 7. Cutting no. 8 from tree *C* made on July 8. Differentiation of summer wood is beginning; ×33.

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* Whitten, J. C., loc. cit.